THE XYRIDACEAE IN THE SOUTHEASTERN UNITED STATES¹

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XYRIDACEAE C. A. Agardh, Aphor. Bot. 158. 1823, "Xyrideae," nom. cons.

(YELLOW-EYED GRASS FAMILY)

Annual or perennial, stemless to caulescent, usually rosulate, scapose terrestrial herbs of high-hydroperiod soils [rarely aquatic]. Roots mostly slender, diffuse-fibrous, with root hairs. Axis sympodial [or monopodial]. Leaves alternate, distichous or spiral, ligulate or eligulate, the bases broad, open-sheathing, frequently equitant and keeled, the blades laterally [to dorsiventrally] compressed, usually flattened, less often terete or ventrally sulcate, the indument usually of uniseriate-glandular, unbranched [to branched] trichomes [or absent]. Inflorescence(s) lateral [to terminal], the scapes 1 to few, arising from axils of scape sheaths [or inner leaves], naked [to short-bracteate], each bearing apically 1 [or more] imbricate-bracted spikes or heads [or a paniculate arrangement of same]. Flowers perfect, 1 to many, solitary and subsessile to pedicellate in the axils of chaffy, leathery, or scarious bracts. Perianth of 2 differentiated whorls. Sepals 3, the anterior (inner) one usually membranaceous and wrapped around the corolla, abscising as the flower opens, the other 2 subopposite, connivent [to basally connate], chaffy, boat shaped, usually keeled, clasping the mature capsule. Petals 3, equal [to unequal], distinct [to united and salverform], strongly clawed, the spreading blades broad, yellow to white [or blue]. Stamens usually 3, epipetalous. Staminodia 3, distinct, clawed as in petals and distally 2-armed, also moniliform-hairy or reduced [or absent]. Anthers 4-sporangiate, bilocular at anthesis, introrsely or laterally dehiscent, dehiscing longitudinally; pollen monosulcate or inaperturate. Gynoecium 3-carpellate, the ovary 1-locular [to incompletely 3-locular], the placentation marginal or parietal [basal, free-central, or axile]; style terminal, tubular, apically 3-branched; stigmas 3, truncated, glandular-hairy; ovules mostly numerous, anatropous, 2-integumented. Fruit

Prepared for the Generic Flora of the Southeastern United States, a project of the Arnold Arboretum currently made possible through the support of the National Science Foundation, under Grant DEB-81-11520 (Carroll E. Wood, Jr., principal investigator). This treatment, the 99th in the series, follows the format established in the first paper (Jour. Arnold Arb. 39: 296–346. 1958) and continued to the present. The area covered by the Generic Flora includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with information about extraregional members of a family or genus in brackets []. References that I have not verified are marked with an asterisk.

The illustration was drawn by Karen S. Velmure from dissections by K. R. Robertson and C. E. Wood, Jr., of material collected by Norton G. Miller in North Carolina.

© President and Fellows of Harvard College, 1983. Journal of the Arnold Arboretum 64: 421–429. July, 1983. capsular, mostly loculicidal; seeds usually numerous, mostly under 2 mm long, with strong longitudinal ridges and finer cross lines, translucent or farinose-opaque, the embryo small, situated at base of an abundant mealy endosperm. Type Genus: *Xyris* L.

A pantropical family of four genera and nearly 300 species, most of them in *Xyris*, the only genus to range into the North Temperate Zone. The remaining genera (*Orectanthe* Maguire, *Achlyphila* Maguire & Wurdack, and *Abolboda* Humb. & Bonpl.) are small and are confined to northern South America.

The family is mainly distinguished by its combination of rosulate and scapose habit; it is also characterized by vessels with simple perforation plates in all vegetative organs; leaves with open sheaths and with narrow blades having parallel or uninerved venation; flowers solitary in axils of (usually) chaffy, imbricate bracts in conelike spicate or capitate inflorescences; perianth trimerous, heterochlamydeous, the sepals with the inside (anterior) member fugacious, membranaceous, and covering the rest of the flower in bud; androecium of 3 epipetalous stamens with anthers opening longitudinally and (usually) 3 staminodia; gynoecium tricarpellate; fruit capsular, typically loculicidal; and seeds small, with copious farinaceous endosperm.

Engler's placement of the Xyridaceae in the large and artificial order Farinosae together with 12 other families showing mealy endosperm and a usually compound superior ovary met with early opposition from many phylogenists. However, there seems to be general agreement in most recent studies that the family is closely related to the Rapateaceae, and both are placed either in the order Xyridales (Hutchinson, 1973) or, more popularly, in the Commelinales (Takhtajan, 1980; Cronquist, 1981; Thorne).

The four genera of Xyridaceae break into two groups (Abolboda and Orectanthe vs. Achlyphila and Xyris) on the basis of foliar and pollen characters. Abolboda and Orectanthe have spinose pollen, appendaged styles, and polystichous leaves with dorsiventral structure and commonly with a hypodermis of colorless cells under both surfaces. Abolboda (ca. 20 species) has an interior sepal that is reduced so that often only the lateral sepals are evident; a corolla that is regular and usually blue; staminodia that, if present, are simple and unbranched; and either styles that are apically three-branched or stigmas that are strongly hairy and trilobed. Orectanthe (O. ptaritepuiana (Steyerm.) Maguire and O. sceptrum (Oliver) Maguire) has three sepals, but the corolla is irregular and yellow, usually strongly curved outward with the interior lobe enfolding the other two lobes in bud; staminodia are lacking; and the style is simple, with the stigma subcapitate.

Achlyphila and Xyris have obviously or obscurely distichous leaves that are usually laterally compressed and lacking the colorless hypodermal layers. Their pollen lacks spines, their styles are unappendaged, and their corollas are regular. The monotypic Achlyphila (A. disticha Maguire & Wurdack) has an elongate, creeping, scaly rhizome from which arise erect, distichously leafy stems; it lacks staminodia and its styles are undivided. Members of Xyris are mostly short stemmed, have an outer sepal much different from the inner two, produce apically bipartite staminodia (in most), and have styles prominently three-

branched above the middle. It is the only genus of the four that produces hairs on the leaves.

Tomlinson believes that, while *Abolboda* and *Orectanthe* are evidently closely related, *Achlyphila* may be a link between *Abolboda* and *Xyris*, thus making it more difficult to consider Abolbodaceae a distinct family, as did Nakai. Before the discovery of *Achlyphila*, Nakai's lead was temporarily followed by Takhtajan (1959).

The family is of little economic importance. Some species of *Xyris* are an important food for the wild turkey (*Meleagris gallopavo*) in the southeastern United States, some others are occasionally used as aquarium plants, and a few species with long scapes and conspicuous spikes are harvested for use in dried plant displays.

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1. Xyris Linnaeus, Sp. Pl. 1: 41. 1753; Gen. Pl. ed. 5. 25. 1754.

Annual or perennial, short- [to prominently] caulescent, usually rosulate, scapose herbs with diffuse fibrous roots, usually perennating by lateral offshoot

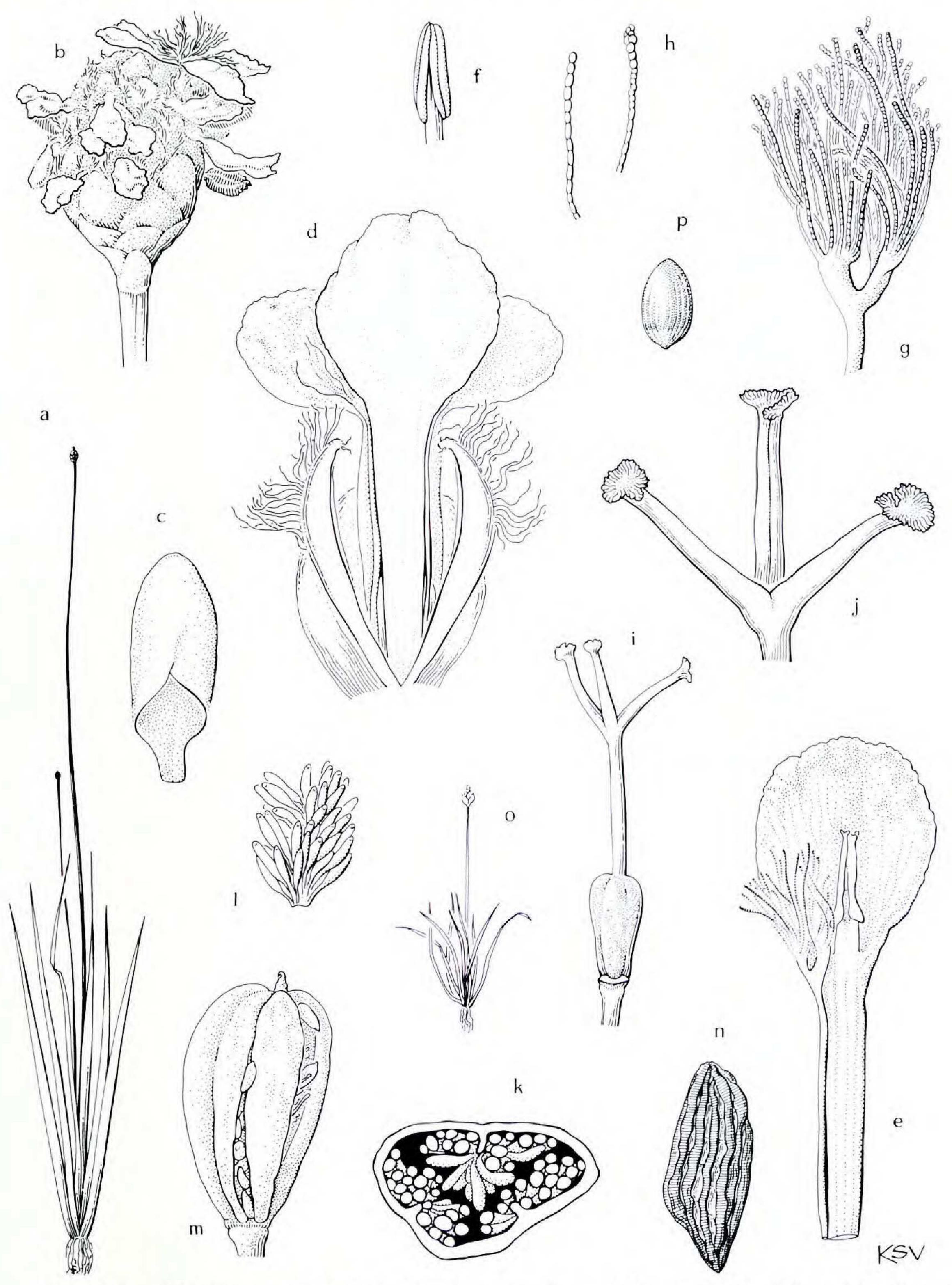


FIGURE 1. **Xyris.** a-n, *X. fimbriata:* a, habit, $\times \frac{1}{8}$; b, inflorescence, with 1 open flower and marcescent corollas of earlier flowers, \times 2; c, inner (anterior) sepal, \times 6; d, flower, from above, showing the 2 fimbriate lateral sepals and the subtending bract below (behind flower), \times 5; e, petal with filament of fertile anther adnate to claw, and staminodium with free filament and much-branched tip, \times 6; f, anther before dehiscence, \times 6; g, tip of staminodium, \times 12; h, moniliform trichomes of staminodium, \times 25; i, gynoecium, \times 5; j, tip of 3-parted style with stigmas, \times 12; k, cross section of ovary, showing numerous orthotropous ovules on 3 parietal placentae, most ovules sectioned, \times 20; l, adaxial side of 1 placenta with orthotropous ovules, \times 12; m, dehiscing capsule, \times 6; n, seed, \times 40. o, p, *X. brevifolia:* o, habit, \times ½; p, seed, \times 40.

buds. Axis sympodial. Foliage externally smooth to variously papillose or rough [to pilose], often bearing uniseriate secretory trichomes on inner surfaces of leaf sheaths. Outer leaves often scalelike; principal leaves mainly linear, equitant, distichous, the sheathing bases open, usually strongly clasping and dilated distally, narrowing gradually or abruptly to junction with blade, there ligulate or eligulate, the sheath edges convergent to form one side, the midrib area the other, of a laterally flattened to terete, angulate or sulcate, usually linear, entire or scabrid [or ciliate] blade. Scapes single or few to a shoot, linear, terete to variously compressed, costate or ancipital, mostly overtopping leaves, each subtended by a sheath leaf that is closed and involute-tubular proximally, open and variously bladed [or bladeless] distally. Inflorescence a terminal, conelike head or spike of tightly to loosely spirally or distichously imbricate chaffy bracts, the lowest usually sterile and smaller than the fertile [less frequently, larger than the fertile and with cusps or blades overtopping the inflorescence], the fertile each with a subsessile axillary flower, sometimes the uppermost again barren. Sepals unequal, the 2 lateral opposing, connivent around the floral base, distinct (or variously connate), chaffy, boat shaped, variously keeled, equilateral or not, the anterior (inner) sepal scarious and enclosing the corolla in bud, fugacious. Petals free [to basally connate], subequal, long clawed, the blades usually broad, yellow [or orange], rarely white, spreading. Stamens equal, the short, fleshy filaments departing just above the petal claw, the anthers basifixed, 2-locular, the pollen monosulcate; staminodia 3, subequal, mostly 2-armed apically, the branches penicillate, with moniliform hairs [rarely glabrous or vestigial]. Ovary 1-locular [to imperfectly 3-locular]; ovules several to many, the placentae marginal or parietal [axile, basal, free-central]; style terminal, slender, tubular, strongly 3-branched above the middle, each branch terminating in a truncate, U-shaped or funnelform stigma fringed with glandular hairs. Capsule usually thin walled, 3-valved, dehiscing along 3 lines alternate with placentae. Seeds small, translucent or farinose, with copious mealy, starchy, proteinaceous endosperm, the embryo small, basal-lateral, the seed coat mostly longitudinally ribbed and cross lined. (Kotsjiletti Adanson, 1763; Xuris Adanson, 1763; Xyroides Thouars, 1806; Jupica Raf., 1836; Ramotha Raf., 1836; Schizmaxon Steudel, 1856.) Type species: Xyris indica L. (Name Greek, in reference to a plant with two-edged leaves, from xyron, a razor.) — Yellow-EYED GRASS.

There are three sections: Pomatoxyris Endl., with possibly 20 species, is characterized by axile placentation and is confined to Australia; Xyris (sect. *Euxyris* Endl.), with ca. 100 species, is distinguished by marginal or parietal placentation and is predominantly pantropic and North American; Nematopus Seub., by far the largest section and morphologically the most diverse, is characterized by basal or free-central placentation and centers in South America. No species are known from Europe, continental Asia, or (except for two species—one North American, one Asian—naturalized in Hawaii) the central or northern Pacific islands.

In the most recent treatment of North American *Xyris* (Kral, 1966), 19 species and three varieties were recorded for continental North America north

of Mexico. One new species has been described since (Kral, 1978), bringing the total to 23 taxa, all of them indigenous and all confined in North America to the eastern United States and Canada. Most are limited to the Coastal Plain, with all but one either restricted to or occurring in the southeastern United States. Only three taxa grow in the wetlands of the Canadian Shield, and of these only *X. montana* Ries is confined to glaciated portions of the continent. Ten species are restricted to the southeastern United States, some as narrow endemics. Two are weeds of New World wetlands; seven center in the lower Coastal Plain terraces of Florida but also occur in the Caribbean (primarily western Cuba) and the pinelands or wet savannas of Belize, Honduras, Mexico, and Nicaragua. Fifteen additional species (five in sect. Nematopus, ten in sect. Xyris) are found in Mexico, Central America, and the Caribbean, with the majority endemic.

Gustaf O. A. Malme, European student of the Xyridaceae and in the early part of the century the recognized authority on *Xyris*, was the last to attempt formal subdivision of sect. Xyris for North America (1937b). He delimited seven subsections, three monotypic and only one (*Mexicanae*) not represented north of Mexico. His artificial classification was based primarily upon characters of the lateral sepals (keels scabrid, ciliate, fimbriate, or villous, vs. keels entire), and secondarily on vegetative characters (e.g., leaf width, leaf length vs. scape-sheath length, degree of fleshiness of leaf-sheath bases). In contrast, the study of Brazilian xyrids by L. B. Smith and R. J. Downs (1968) pays far more attention to vegetative morphology—particularly foliar anatomy and inflorescence characters.

Relatively little has been done with the cytology of North American Xyris beyond some analyses of microsporocytes (Lewis, 1961; Kral, 1966). Twenty taxa have been so studied, and in all the counts have consistently been n = 9. A few root-tip studies (Kral, not yet published) have shown some genomal distinctness.

The flowers of *Xyris* are ephemeral, as is often the case in the Commelinales, with corollas normally not expanded for more than a few hours. Even in the southeastern United States, where several species may cohabit within a small area of wetlands, there may be wide differences between species or species complexes as to time of flowering within a 24-hour period. No nectaries have been found in any species in the genus, and few insects have been observed on the flowers. Only pollen-gathering bees (Bombidae, Andrenidae) have been noted, and to judge from the infrequency of even these visitors to *Xyris* flowers, it has to be concluded that North American xyrids are not obligately insect pollinated. Malme and others have speculated that the primary agent of pollination is wind, but there is considerable evidence (as yet to be tested) that much seed is set apomictically.

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